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NEOTROPICAL MIGRANTS IN UNDISTURBED AND HUMAN-ALTERED FORESTS OF JAMAICA

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ABSTRACT.—Neotropical migrant birds were censused in a variety of natural and human-altered habitats in Jamaica, West Indies. Although power analyses indicated that only differences in abundance >50% were likely to be detected with available sample sizes, we found that total migrant abundance was significantly greater in mangrove and coastal forests than in wet or dry limestone forests. There was no detectable decrease in the total number of Neotropical migrant birds within each forest type as plant biomass decreased with human activity. Species replacements, however, did occur. Common Yellowthroats (*Geothlypis trichas*) increased and other species such as American Redstart (*Setophaga ruticilla*) decreased as vegetation decreased. These results indicate that as a group migrant birds wintering in Jamaica have a wide tolerance for habitat disturbance, but that individual species have specific habitat requirements. Thus, the relative availability of different habitats will affect the abundance of each species. *Received 23 Sept. 1994, accepted 15 May 1995.*

Recent declines in breeding populations of migratory songbirds in North America have been attributed largely to changes in habitat, either in temperate breeding areas or in tropical wintering sites, or in both (Robbins et al. 1989; Askins et al. 1990; Finch 1991; Sherry and Holmes, in press). Winter habitat has been most often implicated in these declines, probably because of the rapidity with which these areas have been deforested in the last two to three decades (Terborgh 1989). This has led to increased interest in the patterns of habitat use by migrants birds during their time in the Neotropics (Keast and Morton 1980, Hagan and Johnston 1992). In particular, it is important to know which habitats these migrant species occupy, their densities, and how their distributions are affected by changes or modifications in habitat due to human activity.

Several recent studies have considered these questions for migrants in

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the Caribbean and in Central America. In the Virgin Islands, Askins et al. (1992) found relatively few migrants in areas where forests had been severely degraded or converted to gardens or forest fragments. In contrast in the Yucatan, Lynch (1992) found comparable numbers and relative abundances of migrant species in areas with traditional forms of agriculture as in natural habitats, but relatively few in pastures created for cattle. In the Greater Antilles, Belize, and Costa Rica, Robbins et al. (1992) also found migrants in plantations of cacao, citrus or coffee, which provided a significant amount of canopy cover and presumably the necessary food resources. In an extensive sampling program in the Caribbean, Wunderle and Waide (1993) showed that some Neotropical migrant species were specialists of mature forests, others used a wide variety of habitats, yet others were specialists of disturbed habitats. The differences observed among these surveys suggests that a thorough assessment of winter habitat for Neotropical migrants requires knowledge for each region.

In this study, we examined the distribution and relative abundance of migrant landbirds during March 1992 in a series of natural and human-altered habitats in Jamaica, W.I. We censused migrants in four kinds of natural forests (dry limestone, wet limestone, coastal, and mangrove) and in several human-altered habitats derived from each of these formations. Differences in bird abundances between natural and derived habitats help assess human impact on the distribution and carrying capacity for these species in Jamaica.

METHODS

Neotropical migrants were censused in widely scattered locations in the western two thirds of Jamaica (west of latitude 76°55′). This region was selected because of concurrent use of satellite imagery to assess vegetation patterns (Confer et al. unpubl. data). We used point counts to estimate bird abundance. All counts were made between 2–29 March 1992, either in the morning (~06:15 to 11:00) or in late afternoon (~16:00 until dark). To reduce the probability of counting the same individual twice, we spaced point counts at ≥100 m intervals in densely wooded areas as did Wunderle and Waide (1993). Hutto et al. (1986) recommended ≥200 m intervals, which we adopted only in open areas such as pasture. Sliwa and Sherry (1992) observed that migrants wintering in Jamaica did not cross territorial boundaries in response to playbacks, and that both American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulescens*) were hyper-dispersed as expected for territorial birds. Furthermore, we obtained more than 50 point counts from four study plots in which more than 75 winter resident Neotropical migrant birds were distinctively color marked (R. T. Holmes and T. W. Sherry, continuing research). Only once was the same banded individual recognized at two consecutive point counts, which shows that replicate counting occurred rarely with point counts 100 m apart in heavily wooded habitat. Moreover, most Neotropical migrant birds in Jamaica occur alone, and rarely in flocks (Lack 1976, Holmes et al. 1989), so that replicate counting of birds for that reason was unlikely.

To detect the maximum number of nearby birds, we used taped calls interspersed with "spshing" (Smith 1975) in the following pattern for each count: 1 min of initial silence –

2 min of tape playback of American Redstart song and chip notes –1 min of spshing –2 min of silence –2 min of Black-throated Blue Warbler song and chip notes –1 min of spshing –1 min of silence. Segments of tapes used by Sliwa and Sherry (1992) were duplicated for playback. Sliwa and Sherry showed that playbacks increased the detection of American Redstarts and Black-throated Blue Warblers by 300 and 230%, respectively, and enhanced the count of some other warbler species. Our emphasis on American Redstarts and Black-throated Blue Warblers complements continuing studies of their winter ecology in Jamaica (Holmes et al. 1989, Holmes and Sherry 1992, R. T. Holmes and T. W. Sherry unpubl data). The attraction of birds to spshing has been documented (Smith 1975), and is well known to birders. Spshing was as loud as possible when no birds were in sight and was reduced as birds approached.

A preliminary list of potential study sites in coastal, mangrove, wet limestone, and dry limestone forests was determined based on descriptions in Asprey and Loveless (1958), Asprey and Robbins (1953), Lack (1976), Loveless and Asprey (1957), Sliwa and Sherry (1993), Wunderle and Waide (1992), and our own field experience in Jamaica. The distribution of Neotropical migrant birds in Jamaica varies with elevation and especially rainfall (Lack 1976, Wunderle and Waide 1993). Thus, to obtain a representative sample of bird abundance, we selected sites with the widest possible range of rainfall and elevation within each habitat type as well as those with intermediate conditions. Rainfall estimates were based on records for December, January and February, the three months preceding the census. Winter is the dry season in much of the Caribbean including Jamaica, and may be a time of food shortage for migrants as discussed by Wunderle and Waide (1993) and as studied in Jamaica by Parrish and Sherry (1994). Census areas in the same forest type were at least 15 km apart. Census points were located at least 50 m from an ecotone, except in a few narrow mangrove and coastal forest stands where they were only 15–25 m from the edge.

Human impact on the density of vegetation was estimated subjectively. At each census point, the density of vegetation was compared visually with that of similar but undisturbed habitat types, and was categorized as follows: 1 = less than 2% reduction in the maximum vegetation caused by humans and their livestock, 2 = 2–33% reduction, 3 = 33–66% reduction, 4 = 67–100% reduction. The biomass at point counts in agricultural or grazed areas was compared to the biomass of natural areas without regard to species composition. For example, coffee plantations were estimated to have 33–66% of the biomass of the original wet limestone forest (categories 2 or 3) even though few of the original plant species were present. Visual estimates were the only feasible method even though they may not as quantitative or as accurate as other more time-intensive methods. Previous use of visual estimates of biomass have been shown to provide sufficient statistical power to discriminate between the similar nesting habitat of Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*) (Confer and Knapp 1981).

A total of 122 point counts was obtained from ten mangrove forest study areas in pure and mixed stands of red (*Rhizophora mangle*), white (*Laguncularia racemosa*), and black (*Avicennia germinans*) mangroves. Most counts were obtained in areas with a canopy height that ranged between 5–15 m: others were in an area with a red mangrove canopy which exceeded 25 m. Black and especially white mangroves grew in higher and drier areas than red mangrove sometimes with stunted and very sparse growth. Some sites contained downed trees, most of which resulted from Hurricane Gilbert in September 1988. Five census counts were on a dike which separated undisturbed forest from a forest completely destroyed by ongoing development. These sites with 50% cover reduction were assigned a human impact value of 3. The total number of counts in each category of human impact, 1–4, was 48, 38, 26, and 10, respectively. No counts were obtained in areas where virtually all mangrove vegetation had been eliminated. A total of 105 point counts was obtained at four census areas of wet limestone forest and in nearby pasture and in plantings of coffee, yams, banana, and coconut that had once been wet limestone forest. In forested areas, current human influence was restricted to selective removal by hand of a few trees, which had a minor impact on the canopy. Canopy of wet limestone forest ranged up to 40 m, and vines and epiphytes were abundant. Point counts in the valleys were located in pasture land and agricultural plantings, and some included small clusters of trees or wooded fence rows. The number of counts in each category of human impact, 1–4, was 34, 17, 8, and 46, respectively. We counted birds at 112 points in five census areas of dry limestone forest. Ten xeric sites had a cactus, thorn-scrub community (Asprey and Robbins 1953) dominated by columnar cactus (*Stenocereus hystrix*) and thorn acacia (*Acacia tortuosa*). Evergreen seasonal forest (Beard 1944) with a canopy to 20 m, having some foliage reduction during the dry season and abundant lianas and epiphytes occurred at the least xeric sites. Overgrazing and cutting of forests for firewood was widespread, producing scrub, or ruinate, habitat in areas probably once forested. In most disturbed sites the dominant vegetation was thorn acacia occasionally mixed with columnar cactus. For the four categories of human impact, 1–4, the number of counts was 43, 17, 28, and 24, respectively. We made 15 counts at five areas in coastal forests on slight elevations characterized by a wide variety of plant associations. These frequently were dominated by palms (*Sabal jamaicensis*) and logwood (*Haematoxylon campechianum*) and other shrubby vegetation, along with stands of taller trees such as red birch (*Bursera simaruba*) and burnwood (*Metopium brownii*). At several sites, coastal forests graded into mangrove forests or dry limestone forests, and some birds may have moved among these habitats.

Statistical tests were performed with SYSTAT®, excepting a few chi-square tests. Group comparisons were screened for homogeneity of variances with Bartlett's test. If the variances were not homogeneous, the data were transformed by log, square root, or arc-sine functions. If the initial or transformed variances were homogeneous, tests for differences among groups used a one-way ANOVA. The sum probability of a Type I error for all group comparisons was set at 5% with a Tukey-Kramer adjustment for unequal sample size. If variances remained significantly different despite transformation, we used Kruskal-Wallis or Mann-Whitney *U*-tests. Comparisons of bird abundance among categories of human-caused reduction in vegetation used data pooled for category 1–3 to obtain larger sample sizes. Differences in abundance between the pooled counts and point counts at category 4 were tested with a Student's t statistic. Power analyses (Cohen 1987) of the data were performed to determine the ability of our data to detect significant differences (see below).

RESULTS

A total of 704 Neotropical migrant birds of 16 species observed at 354 point counts averaged 2.0 individuals per point. Paruline warblers comprised >99% of the migrants. Six species were observed at more than 50 points (Fig. 1): American Redstart (162 individuals), Prairie Warbler (*Dendroica discolor*) (101), Northern Waterthrush (*Seiurus noveboracensis*) (89), Black-and-White Warbler (*Mniotilta varia*) (68), Black-throated Blue Warbler (58), and Common Yellowthroat (75). Other species were Northern Parula (*Parula americana*) (55), Palm Warbler (*D. palmarum*) (28), Magnolia Warbler (*D. magnolia*) (14), Cape May Warbler (*D. tigrina*) (12), Worm-eating Warbler (*Helmintheros vermivorus*) (10), Ovenbird (*Seiurus aurocapillus*) (6), Prothonotary Warbler (*Protonotaria ci-

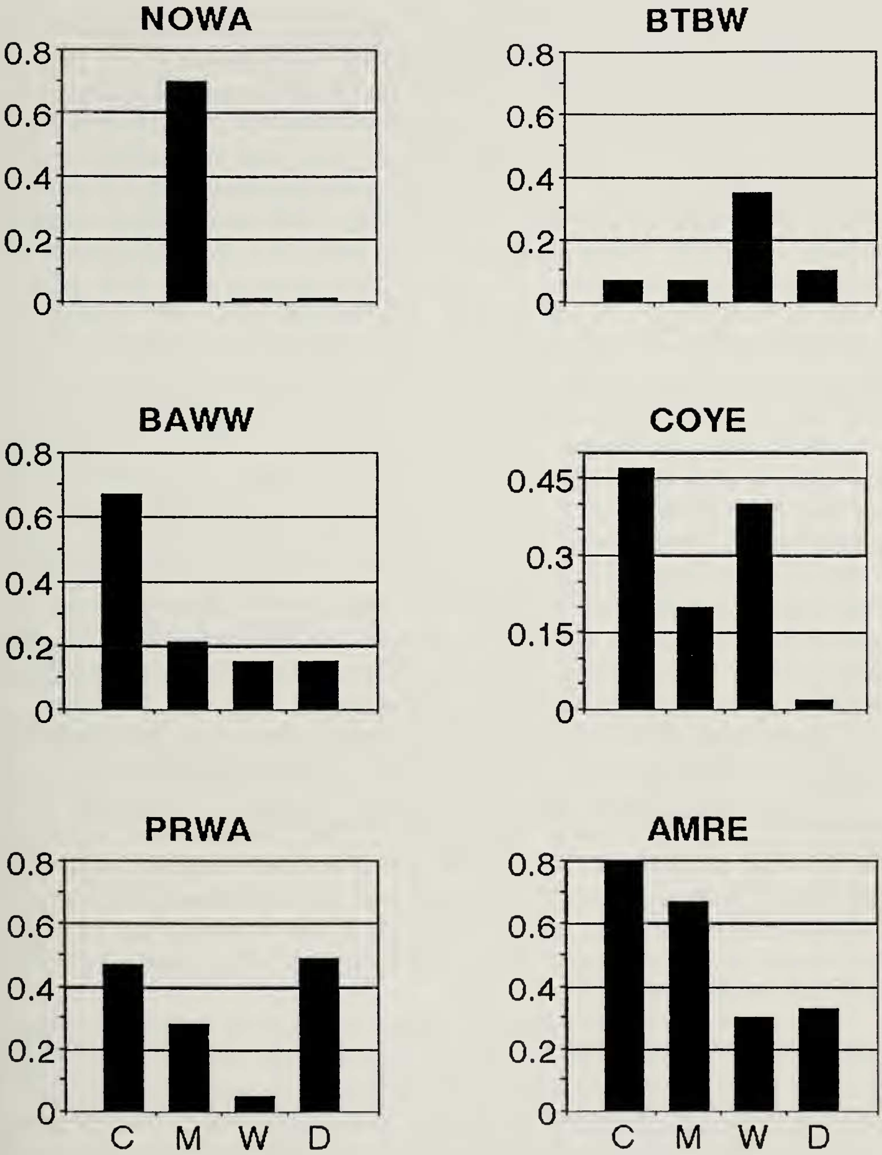

FIG. 1. Distribution of some common Neotropical migrant birds in Jamaica. Values are the mean of all point counts in each of four forest types. C = coastal; M = mangrove; W = wet limestone; D = dry limestone forests; NOWA = Northern Waterthrush; BTBW = Black-throated Blue Warbler; BAWW = Black-and-white Warbler; COYE = Common Yellowthroat; PRWA = Prairie Warbler; and AMRE = American Redstart. Note change of scale for COYE.

trea) (3), Indigo Bunting (*Passerina cyanea*) (2), Yellow-throated Vireo (*Vireo flavifrons*) (1), Hooded Warbler (*Wilsonia citrina*) (1).

Many of our comparisons were based on small sample size and showed only minor differences between means, increasing the chances of a Type II statistical error. A power analysis of our data used the number of migrants detected per point count for human impact categories 1–3 pooled vs category 4 for the three forest types with >100 point counts (coastal forests excluded). Power analyses of the difference in total number of Neotropical migrants among the forest types showed a 46–88% probability of detecting a true difference of ≥50% (Table 1). A 30% difference in total Neotropical migrant birds would be detected as significant in less than 10% of similar trials. Comparisons of individual species involved far fewer individuals per point count, and the power analyses show that for these data a difference of 50% was likely to be detected only for sample sizes of many hundreds to thousands of point counts. No studies to date have achieved such sample sizes for a within-habitat analysis of the effect of human disturbance on migrant bird abundance. Our sample sizes of 105–122 point counts of total Neotropical migrants for each habitat may be as sensitive as previous studies but are likely to detect a statistically significant difference only for true differences ≥50% (see Discussion). Tests for individual species are likely to show a difference only for major changes in relative abundance.

The total number of Neotropical migrant birds per point count for both mangrove forests (mean ± *SE* 2.53 ± 0.17), and coastal forests (3.67 ± 0.58) were significantly higher than those for wet limestone forests (1.43 ± 0.11) or dry limestone forests (1.70 ± 0.16) (Tukey-Kramer one-way ANOVA, $P < 0.01$). The total number of Neotropical migrant birds were indistinguishable for mangrove forests and coastal forests and for wet limestone forests and dry limestone forests. Coastal forests had the highest counts of Neotropical migrant birds, but the sample size was small and the variance high.

Northern Waterthrushes occurred almost exclusively in mangrove forests (Fig. 1), as observed by others (Wunderle and Waide 1993). They were the most habitat-specific species detected at more than 50 point counts. Most waterthrushes occurred within sight of water. Our censuses were conducted at the end of the dry season by which time standing water was visible at only 63% ($N = 82$) of the mangrove forest point counts. The mean number per point count with and without water was 0.99 and 0.22, respectively, a highly significant difference ($t = 5.835$, $P < 0.001$, after square-root transformation).

American Redstarts were common in all forest types (Fig. 1), although their densities in mangrove and coastal forests were significantly higher

TABLE 1

DETECTION OF HUMAN INFLUENCE ON BIRD ABUNDANCE

Habitat	Calculated[a,b]	Bird species[c]					
		NTMB	PRWA	BAWW	AMRE	COYE	BTBW
Mangrove forests							
For 30% change and							
observed N = 113 and 9	Power:	0.20	0.08	—	0.12	<0.06	<0.06
observed variance and power = 0.9	N:	132	>1000	—	350	>1000	>1000
observed variance and power = 0.8	N:	99	980	—	240	>1000	>1000
For 50% change and							
observed N = 113 and 9	Power:	0.46	0.11	—	0.25	0.07	0.07
observed variance and power = 0.8	N:	38	262	—	82	1335	1335
Dry limestone forests							
For 30% change and							
observed N = 85 and 27	Power:	0.32	0.15	0.10	0.17	—	—
observed variance and power = 0.9	N:	210	540	>1000	470	—	—
observed variance and power = 0.8	N:	160	390	>1000	360	—	—
For 50% change and							
observed N = 85 and 27	Power:	0.66	0.33	0.16	0.38	—	—
observed variance and power = 0.80	N:	58	145	371	122	—	—
Wet limestone forests							
For 30% change and							
observed N = 59 and 46	Power:	0.40	<0.08	0.08	0.13	0.1	0.2
observed variance and power = 0.9	N:	160	>1500	>1500	>1000	>1500	500
observed variance and power = 0.8	N:	122	>1500	1600	980	1340	360
For 50% change and							
observed N = 59 and 46	Power:	0.88	<0.08	0.10	0.26	0.17	0.44
observed variance and power = 0.8	N:	43	>1000	621	284	393	129

[a] The calculated power is the probability of detecting a specified change at the 95% confidence level comparing highly disturbed sites to all others given the observed sample sizes.

[b] The calculated N is the number of counts, equally divided between highly disturbed sites and all others, necessary for the specified probability of detecting a specified change at the 95% confidence level given the observed variance.

[c] NTMB = Neotropical migrant birds; PRWA = Prairie Warbler; BAWW = Black-and-white Warbler; AMRE = American Redstart; COYE = Common Yellowthroat; BTBW = Black-throated Blue Warbler.

than in wet or dry limestone forests (Tukey-Kramer one-way ANOVA of ln transformed data, $P < 0.05$). Black-and-white Warblers were widespread, but occurred in significantly greater density in coastal forests than in any other habitat (Tukey-Kramer one-way ANOVA of ln transformed data, $P < 0.05$). Chi-square 2×3 contingency analyses showed significant differences in frequency of detection among forest types for the following species: Common Yellowthroats, rare in dry limestone forests (chi square = 49, $P < 0.001$); Prairie Warblers, rare in wet limestone forests (chi square = 29, $P < 0.001$); and Black-throated Blue Warblers, moderately abundant only in wet limestone forests (chi square = 37, $P < 0.001$) (Fig. 1).

Our observations of the differences of bird density with respect to human-caused reduction of vegetation suggest that only sites with extreme disturbance are likely to have significant reductions in bird abundance (Fig. 2), while the power analyses suggested that only comparisons among large samples would be likely to detect any difference. Consequently, we pooled results for category 1–3 and compared these to category 4.

Human influence had little effect on total Neotropical migrants per point count within each major habitat (Fig. 2). The coefficient of variation for each forest type derived from the means of the total number of Neotropical migrants for each category of human influence varied by only 6.0–18.6%. *t*-tests showed no significant difference in total Neotropical migrant birds between categories 1–3 combined and category 4 for each forest type.

Point counts for mangrove forests at sites with very little vegetation (category 4) still had a large total number of migrants (Fig. 2). However, mangrove point counts could not be obtained in areas that were totally denuded because construction activities prevented access. We believe paruline warblers would have been extremely rare in such sites. None of the six most common species had a detectable difference in abundance in mangrove forests when categories 1–3 were pooled and compared with category 4 ($P > 0.05$). Black-and-white Warblers were the only species that showed a decline in moderately disturbed mangrove; chi-square analysis of all four categories for Black-and-white Warblers showed a highly significant difference (chi square = 17, df = 3, $P < 0.001$).

Human impact in areas of former wet limestone forests produced a heterogeneous habitat including a very diversified agriculture. The total number of Neotropical migrants was statistically indistinguishable comparing categories 1–3 with category 4 ($P > 0.05$). Some category 4 counts in areas which were not denuded and which had a forest edge, actually had a high density of Neotropical migrant birds. Among individual species, American Redstarts declined ($t = 2.18$, $P = 0.032$ using square-root

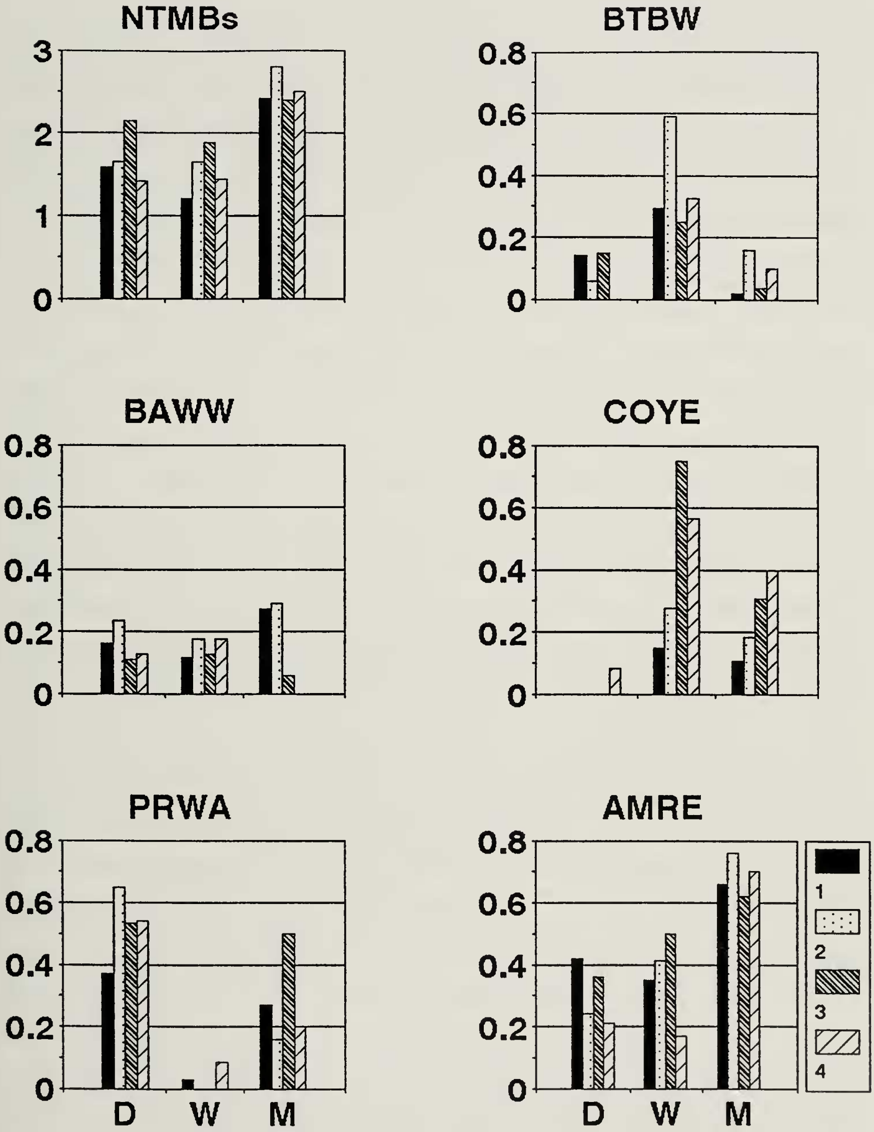

FIG. 2. Distribution of Neotropical migrant birds related to human disturbance. Histograms show mean abundance per point count for four categories of human impact for each of three habitats. NTMBs = Neotropical migrant birds. Other abbreviations and categories as in Fig. 1. Note change of scale for NYMBs.

transformation) and Common Yellowthroats increased (t = 2.214, P = 0.029) comparing point counts with the most extensive reduction in biomass to all others. Sliwa and Sherry (1993) observed that the detection of Common Yellowthroats was decreased by taped playbacks of American Redstarts and Black-throated Blue Warblers. However, we observed that spshing produced responses from many birds which were undetected until spshing started, especially Common Yellowthroats.

Human impact on dry limestone forest seemed to be greater than for any other habitat in our study areas. Eight counts were taken in areas with nearly a 100% reduction in biomass due to housing construction or extreme cutting plus overgrazing. No Neotropical migrant birds were observed during these counts. Despite the absence of Neotropical migrant birds under these extreme conditions, when these counts are pooled with other category 4 counts with little vegetation, no effect of human activity on total Neotropical migrant birds was detected (t = 0.896, P = 0.372). Two species that occurred at ≥50 point counts showed an absolute difference in abundance related to human impact on dry limestone forest. Black-throated Blue Warblers were present only in category 1–3, whereas Common Yellowthroats were present only in category 4. But with their infrequent occurrence and resultant small sample size, these differences were not statistically significant (chi-square, $P > 0.05$).

DISCUSSION

Few of our comparisons showed significant differences in abundance of Neotropical migrants related to the extent of habitat alteration caused by human activity. Two sampling factors probably contributed to this result (1) the sampling protocol, and (2) the limited statistical power of point counts. Our category 4 areas could have as much as ⅓ the biomass of undisturbed habitat. Some locations with a biomass of slightly less than ⅓ the original still had high counts of Neotropical migrant birds. Although sites denuded of vegetation contained few if any birds, category 4 sites as a whole did not show a decline in total number of Neotropical migrant birds. Furthermore, our sampling did not distinguish among the different kinds of crops or agricultural practices. Significant differences in bird distribution among different types of agriculture have been recorded elsewhere (Wunderle and Waide 1993). Documentation of such differences in Jamaica requires additional study with an alternative sampling design. The power analyses showed that comparisons within a single species have little ability to detect differences in abundance (Table 1). Only sample sizes of several hundred to over a thousand point counts, depending on the amount of change in abundance, were likely to show statistical significance. The limitations revealed by power analyses for our data provide insight about the statistical sensitivity of other studies that also used point counts to study Neotropical migrant birds. For our counts of Neotropical migrants, the coefficients of variation in mangrove forests, dry limestone forests, and wet limestone forests were <1. Wunderle and Waide (1992) observed fewer Neotropical migrant birds per point count with higher standard deviations and coefficients of variations >2. Thus, their data had less power than ours for the same sample size. Our results more closely approximate those of Sliwa and Sherry (1993) who reported a coefficient of variation less than one using playback recordings to sample American Redstarts and Black-throated Blue Warblers. Studies that use playbacks may obtain a more accurate census of territorial and hyperdispersed birds, reducing the variance and increasing the statistical power of the test.

While acknowledging the sampling limitations described above, we believe the results of this study indicate clearly that Neotropical migrant birds as a group occur widely in many habitats in Jamaica, including second growth, agricultural areas and other areas modified by human activity. Migrants were present in virtually every habitat that contained shrubby or woody vegetation and hence provided cover and food. Different species, however, preferentially occupied different habitats, e.g., American Redstarts were most common in mangroves, Black-throated Blue Warblers in undisturbed wet limestone forests, Common Yellowthroats in disturbed wet limestone forests, Prairie Warblers in dry limestone forests, and Northern Waterthrush in wet mangrove forests. Some species increased in abundance as forest canopy was thinned. Common Yellowthroats, in particular, increased in all three major forest types, although this increase was significant only in wet limestone forests. Palm Warblers, although too rare for analysis, occurred exclusively in category 4 point counts in all three major forest types, whereas none was recorded at any point with more vegetation. During casual observations, we noted Palm Warblers in disturbed habitats throughout Jamaica, as did Wunderle and Waide (1993).

These findings indicate that Neotropical migrants as a group have a wide tolerance for habitat disturbance, but that different species respond in different ways. Thus, as vegetation is reduced but not eliminated, habitat for Common Yellowthroats and perhaps Palm Warblers increases, while that for Black-and-White Warblers and Black-throated Blue Warblers decreases. The relative proportions of such habitats will determine the abundances of these species in their wintering areas. Conservation efforts will need to take such species-specific habitat requirements into account when developing management plans.

Point counts reveal only the patterns of abundance of migrant birds among habitats. Abundance, however, might not either reflect survivorship in each habitat throughout the winter (van Horne 1983, see Sherry and Holmes, in press), or the ability of each habitat to prepare birds for northward migration. Different habitats, especially degraded ones, may be less suitable in terms of providing sufficient cover for overwinter survival or food. Further studies are needed to examine habitat-specific survival rates and other measures of fitness in migrant birds in winter. Such information will be useful in evaluating the long-term effects of habitat destruction and degradation on migrant bird populations and for developing conservation plans.

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